

XXIV. *On some of the principal Mimetic (Müllerian) Combinations of Tropical American Butterflies.* By J. C. MOULTON, F.E.S., of Magdalen College, Oxford.

[Read June 3, 1908.]

PLATES XXX—XXXIV.

IN the year 1896 Mr. W. F. H. Blandford, with the help of the late Mr. Osbert Salvin, F.R.S., selected a series of mimetic combinations of Tropical American butterflies from the Godman-Salvin collection. These he exhibited in the same year at the Royal Society and at the Entomological Society of London (Proc. Ent. Soc. Lond., 1896, p. xxxviii). They were also shown and described by him in the following year, during the discussion which followed Dr. F. A. Dixey's paper on "Mimetic Attraction" (Proc. 1897, pp. xx-xxxii and xxxiv-xlvii; Trans. 1897, pp. 317-331). The opinion was strongly expressed at the time that it would be of great advantage if the associations could be kept intact, or at least some permanent record of them preserved. As regards the great majority of specimens exhibited by Mr. Blandford this was found to be impracticable; but Professor Poulton, F.R.S., at once began to collect material for similar groups—from the Hope Collection, from the great series of duplicates presented to the Hope Department by Dr. F. Ducane Godman and Mr. O. Salvin, and from other sources. By 1901 so much progress had been made that he applied to Dr. Godman for his kind help in lending the comparatively few rare species which did not exist in the Hope Department. These were added to the Oxford material, and beautiful photographs of four South American combinations (Plates XXX-XXXIII) were taken by Mr. Alfred Robinson of the Oxford University Museum. In order to give some conception of the analogy between Müllerian resemblances in the Old World and the New, a group of Oriental *Euplainæ* with one convergent Danaine was photographed at the same time (Plate XXXIV). The South American associations, of which a permanent record was thus made, are

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as follows, tabulated according to their geographical distribution:—

1. North-Central America (Guatemala, Honduras, and Nicaragua); shown on Plate XXX.
2. East Brazil; shown on Plate XXXI.
3. Upper Amazons (Ega); shown on Plate XXXII.
4. Ecuador, Peru, and Bolivia; shown on Plate XXXIII.

The half-tone blocks for these plates were prepared shortly afterwards by Messrs. André and Sleigh; but in the press of other work Professor Poulton has been unable to publish an account of the material or to describe the plates. Early in the present year he invited me to undertake this task, which I need hardly state has proved an extreme pleasure, in view of the exceptional interest of these mimetic associations. I would here like to take this opportunity of recording my sincere gratitude to him, first, for allowing me the privilege of writing this paper, and secondly, for all the kind help and trouble he has shown in assisting me to produce it. The difficulties of a first entomological paper, so alarming to the beginner, have all been made easy by his kindly surveillance. The following associations, although arranged in a different order, are reproduced with but little change from Mr. Blandford's paper (*Proc. Ent. Soc. Lond.*, 1897, pp. xxii-xxvii): it will be noted, however, that while his combinations were wholly composed of butterflies, certain examples of *Heterocerous* mimics, as well as a few additional *Rhopalocera*, have been incorporated in the tables of the present paper. Mr. Blandford spoke of these mimetic associations as "groups," but I have adopted Professor Poulton's suggestion that they should be called "associations" or "combinations."*

In the tabular form in which the associations are set forth below, the *Ithomiine* models are shown on the left and their mimics on the right; the whole series forming a large combination with a single type of pattern.

* "Essays on Evolution," 1908, Essay X, p. 293:—"In this essay the word 'group' is employed to express an arrangement based on affinity, the word 'combination' or 'association' to express an arrangement founded on bionomic relationship. Thus a genus or family is spoken of as a group, a set of Müllerian models and mimics as an association or combination."

COMBINATION I. (Shown on Plate XXX.)

North Central American Type—Guatemala, Honduras
and Nicaragua.

ITHOMINÆ.

Tithorea sp.

Melinæa imitata, Bates
(Figs. 1 and 2).

Mechanitis doryssus, Bates
(Figs. 3 and 4).

Mechanitis lycidice, Bates

Ceratinia dionæa, Hew. (Figs.
5 and 6).

Ceratinia fenestella, Hew.
(Figs. 7 and 8).

DANAINÆ.

Lycorca atergatis, Doubl. and
Hew. (Figs. 13 and 14).

NYMPHALINÆ.

Protogonius cecrops, Doubl.
and Hew. (Figs. 21 and 22).

Eresia phillyra, Hew. (Figs.
19 and 20).

HELICONINÆ.

Heliconius telchinia, Doubl.
and Hew. (Figs. 9 and 10).

Eucides zorcaon, Reak. (Figs.
11 and 12).

PIERINÆ.

Dismorphia praxinæ, Doubl.
(Figs. 17 and 18).

*Perrhybris (Mylothris) ma-
lenka*, Hew. (Figs. 15 and
16).

HYPSIDÆ (Moth).

Pericopsis angulosa, Walk.

The only addition to Mr. Blandford's list, except the Pericopid moth, is *Mechanitis lycidice*, Bates, which this authority places in an intermediate position between the above North Central-American and a South Central-American (Costa Rica to Panama) combination. He includes four other species in this intermediate position, but these are so much nearer to the southern combination that no mention of them is necessary here. *M. lycidice*, however, is extremely variable, and, in Guatemalan specimens, the black bar of the hind-wing is as a rule well developed, as in the northern Müllerian association. On the other hand, the absence of this feature in many Costa Rican examples permits their introduction into the southern combination.

It will be seen from the accompanying Plate XXX that the general pattern of this association consists of a conspicuous light brown (fulvous) ground colour, crossed by parallel black bands and oblique bars, the apex of the fore-wing being relieved by two yellow bars between the last-mentioned black markings. While it is apparent that all the members of this association have gradually become drawn together into one general pattern, we can also clearly see how single constituent species have followed others in minor characteristics. A specially remarkable illustration of this is afforded by the strong resemblance between *Melinæa imitata* (Figs. 1 and 2) and *Heliconius telchinia* (Figs. 9 and 10). Here, the broken yellow sub-apical bands of the *Melinæa* are closely followed by those of the *Heliconius*. On the under side of the fore-wing, an irregular series of white spots appears along the hind margin of the *Melinæa*, and similar spots are present although very faintly developed and more marginally placed along the anal portion of the hind margin in the *Heliconius*. The same likeness is found along the hind margin of the hind-wing, where however the usual radiating white streaks of the *Heliconius* are shortened into a rough resemblance to the rounded or oval spots of the *Melinæa*.*

The exceptionally close resemblance between two such widely different genera as *Melinæa* and *Heliconius*, as exemplified by *M. imitata* and *H. telchinia*, affords a good instance of the entire independence of affinity and mimicry, as Professor Poulton points out in "Essays on Evolution," 1908, p. 235. Thus two Ithomiine genera (*Mechanitis* and *Ceratinia*), with four different species (including *M. lycidice*), bear a general likeness to the *Melinæa* pattern, and yet none of them afford nearly so close a resemblance as that exhibited by the *Heliconius*. Hence the Ithomiine genus *Melinæa* is far more closely resembled by its Heliconine mimic belonging to a very different sub-family, than by any Ithomiine which contributes a member to the association. Similarly the *Heliconius* bears a much closer likeness to the Ithomiine model than to the nearly allied *Euclides*.

My attention was directed by Professor Poulton to the fact that the second Heliconine of this association, *Euclides zorcaon* (Figs. 11 and 12), also presents in one special detail a resemblance to the Danaine, *Lycorea atergatis*

* See Poulton, "Essays on Evolution," 1908, p. 350.

(Figs. 13 and 14), in this respect its probable model. I refer to the peculiar ochreous colouring of the oblique markings in the fore-wing apical region,—markings which are of a bright yellow tint in nearly all the other constituents of the combination. It should be noted, however, that ochreous markings in this region are characteristic of many species of both *Eucides* and *Lycorea*. As regards their form, the pale markings of the fore-wing present certain similarities in these two species. An irregular somewhat hour-glass-shaped spot appears at the end of the cell of each species, as also an elongate spot with a median constriction near the anal angle. The form of these and the other markings is very variable, but their general likeness is noticeable. It will be found in other combinations considered in the later pages of this paper that the species of *Protogonius* are generally specially associated with those of *Lycorea*. Thus in the present instance *P. cecrops* (Fig. 21) not only possesses the ochreous markings towards the apex of the fore-wing, but the marginal hind-wing spots are more strongly developed on the upper surface than in any other species of the association except *Lycorea atergatis*.

Ochreous bars also appear in the female of the Nymphaline, *Eresia philyra* (Fig. 20), which in other respects has evidently been drawn after *Ceratinia dionæa* (Fig. 6), with its row of distinct yellow spots along the hind margin of the fore-wing. Interesting features of the male *Eresia* (Fig. 19) are the narrow hooked fore-wing, and the absence of special paleness in the apical markings, both suggesting the influence of some *Dione* or *Eucides* (perhaps *E. aliphera*, Godt.).

Dismorphia praxinæ (Figs. 17 and 18) presents several points of interest. First, the size and general shape suggest *Mechanitis doryssus* (Figs. 3 and 4) as the model, as was pointed out by Godman and Salvin :—“The female has a colour resemblance to *Mechanitis doryssus*, a species abundant throughout the same area” (“*Biologia Centrali-Americana, Rhopalocera*,” 1887–1901, Vol. II, p. 176). On the other hand, the yellow apical markings follow far more closely those of *Melinæa imitata* (Figs. 1 and 2), and its mimic, *Heliconius telchinia* (Figs. 9 and 10), especially the latter. The dark bands of both wings correspond more nearly with those of the *Heliconius* than with the narrower markings of the *Mechanitis*.

The *Perrhybris* (Figs. 15 and 16) can only be regarded

as an outlying member of the association; for the male (Fig. 15) does not mimic at all on the upper surface, while the female (Fig. 16) is rather a rough mimic, the wings being comparatively broad and the dark median band of the hind-wing but feebly developed. The mimicry of the under surface of the male *Perrhybris* is discussed by Dr. F. A. Dixey in *Trans. Ent. Soc. Lond.*, 1894, pp. 286 and 320; 1896, pp. 67-72. It is characteristic of this genus, that while invariably entering a Müllerian association, it never presents more than a rough mimetic resemblance. The peculiar serration of the inner border of the deep black hind-wing margin in the female is discussed on p. 594.

The moth (*Pericopis*) is also but a rough mimic; for in it no black median band crosses the hind-wing, although the marginal border is of much greater breadth, and thus the unbroken discal space of ground colour is barely noticeable.

Evidence that members of this association frequent the same locality and may be mistaken for one another by the captor, exists in the Hope Department, where one *Melinæa imitata*, two *Heliconius telchinia*, and an example of the moth, *Pericopis angulosa*, all taken in Honduras in 1895, had been put together as a single species!

A general survey of the association shows that the closest resemblance exists between *Melinæa imitata* and *Heliconius telchinia*. A second pair—although not nearly so close—is provided by *Lycorea atergatis* and *Euwides zorcaon*; a third by *Ceratinia dionæa* and *Eresia phillyra*, ♀. Lastly, *Dismorphia praxinoe* ♀ presents a general resemblance to *Mechanitis doryssus*, *Melinæa imitata* and *Heliconius telchinia*. The *Perrhybris* and moth are, as previously stated, only rough mimics of the same pattern.

COMBINATION I. A.

The Guiana Type. British, Dutch and French Guiana.

A detailed account of this association is unnecessary; for it has been described in much detail and illustrated with many beautiful plates by Mr. W. J. Kaye, F.E.S. (*Trans. Ent. Soc. Lond.*, 1906, p. 413). A Nymphaline member, *Eresia eunice*, Hübn., was however accidentally omitted by this naturalist, who has now kindly provided me with the following interesting note on it:—"Up till the date of my paper, October 1906 (*Trans. Ent. Soc. Lond.*, 1906, p. 413), I had received about twenty-five specimens of this species. None of the specimens show

any tendency to melanic hind-wings, but the females are certainly more heavily barred than the males. The latter show a strong tendency to a breaking up of the bar into a series of spots much as in the male of *Eucides nigrofulva*, Kaye, *vide* Pl. XXIII, fig. 13. I do not expect that *Eresia eunice* usually sits with the *Melinæas*, etc., on the white flowers of *Eupatorium macrophyllum*, because I have stopped Roberts sending collections from off these flowers, but still I get a fair number of *E. eunice*. There is not the slightest doubt however that it is a member of the group and derives its colouring therefrom."

COMBINATION II.

The East Brazilian Type.

This type is split up by Blandford into two sub-divisions, (a) with yellow apical spot or spots in fore-wing. (b) With white markings in the same position. The following table shows the constituent species arranged as in Combination I.

(a) *The apical spots on the fore-wing yellow.*

ITHOMIINÆ.

Tithorea, sp.

Melinæa ethra, Godt.

Mechanitis nesæa, Hübn.

Napeogenes xanthone, Bates.

Ceratinia laphria, Doubl.

DANAINÆ.

Lycorea halia, Hübn.

NYPHALINÆ.

Eresia esora, Hew.

Eresia, sp.

HELICONINÆ.

Heliconius dryalus, Hopff.

Eucides dianasa, Hübn.

PIERINÆ.

Dismorphia astynome, Dalm.

(b) *The apical spots on the fore-wing white. (Shown on Plate XXXI.)*

ITHOMIINÆ.

Mechanitis lysimnia, Fabr.

(Figs. 1 and 2).

Napeogenes euryanassa, Feld.

(Figs. 5 and 6).

Ceratinia daeta, Boisd. (Figs.

3 and 4).

NYPHALINÆ.

Protogonius drurii, Butl.

(Figs. 10 and 11).

HELICONINÆ.

Heliconius narcæa, Godt.

(Figs. 7 and 8).

Heliconius polychrous, Feld.

(Fig. 9).

In sub-division (b) another *Heliconius*, *H. polychrous*, Feld., and a Nymphaline, *Protogonius drurii*, Butl., have now been added to Blandford's list.

The principal characteristics of this association are the presence of a broad yellow band parallel to the costal border of the hind-wing, and an oblique bar crossing the fore-wing and passing from near the centre of the costa towards the hind-margin. This nearly median bar is succeeded by a large apical spot, or group of spots, sometimes yellow [sub-division (a)], and sometimes white [sub-division (b)].

Sub-division (a). In this association the Danaine, *Lycorea habia*, affords a striking resemblance to *Melinæa ethra*, although the hind-margin of the hind-wing has not lost its border of white spots. As noticed in Combination I, the *Lycorea* possesses a buff or ochreous tint in place of the usual bright yellow markings so typical of this association.* It is also noteworthy that the yellow of the *Melinæa* is slightly duller than that of the association generally. *Mechanitis ncsæa*, besides being smaller, differs slightly from the *Melinæa* in having two small yellow sub-apical spots in addition to the yellow apical patch; there is also a far smaller development of black markings on the basal side of the yellow in the fore-wing; but in spite of these differences the superficial resemblance is very close.

A very good Pierine mimic, *Dismorphia astynome*, enters this association, having in the female the yellow apical spot just as in *Melinæa ethra*. It has furthermore acquired the typical Ithomiine shape with narrow wings. The yellow bar of the hind-wing is not strongly developed, but sufficiently to bring the species well within the combination. The male also has followed the female into the association; although here the hind-wing band is far less yellow and the ancestral white still prevails in the costal area of the hind-wing as in the male of *D. praxinæ*. As in this latter species, the white patch is almost certainly hidden in flight and at rest. The male lacks the apical spot of the fore-wing, although a slight suggestion of it is indicated by a few yellow scales in that region.

* The hind-wing band is not nearly so bright in the *Lycorea* as in other members of the association. Prof. Poulton has given reasons for the belief that the tint may have been even duller about eighty years ago. See Ann. Mag. Nat. Hist., ser. 7, vol. xiii, 1904, pp. 359, 360.

An interesting point emerges in connection with the ancestral white of *Dismorphias* of this pattern. Besides the white portion on the upper side of the hind-wing mentioned above, a white patch occupies the inner marginal area of the fore-wing under side. The meaning of this retention of the white on parts of the surface hidden by the overlapping of the wings is very clearly explained and illustrated by Professor Poulton in his paper "Natural Selection the Cause of Mimetic Resemblance and Common Warning Colours," Linn. Soc. Lond., Journ. Zool. vol. xxvi, p. 606, pl. 40. In addition to the white patches, there are other distinct traces of the ancestral white on the under side of both wings. These persistent traces are formed by a few white scales—easily visible to the naked eye—near the hind margin of the hind-wing and especially at the apex of both wings. The general appearance of the under side suggests that it may possess a cryptic significance, which is an argument against the unpalatability of this Pierine.*

Sub-division (b). All the *Ithomiines* resemble each other except for the fore-wing apical markings (Plate XXXI, figs. 1–6). *Heliconius narcæa* (Figs. 7 and 8) perhaps follows *Mechanitis lysimnia* (Figs. 1 and 2) more closely than it does any of the other *Ithomiines* of this sub-division: its likeness to *Melinæa ethra* of sub-division (a) is far stronger. The *Mechanitis* does not exhibit that tendency towards transparency which is so characteristic of large numbers of the *Ithomiinæ*, and is readily noticeable in the *Ceratinia* (Figs. 3 and 4) and *Napeogenes* (Figs. 5 and 6) belonging to this combination. *Heliconius polychrous* (Fig. 9) must be considered a rough mimic. Its principal defect, which is not very apparent in the figure on Plate XXXI, is the great reduction of the tawny colour and the corresponding increase in the black and yellow markings of both wings. *Protogonius drurii* (Figs. 10 and 11) again is a poor mimic, as is customary in that genus. It is, as is also usual in the genus *Protogonius*, the only member of its association with an obviously and strongly cryptic under surface. The yellow band across the hind-wing is easily traceable, although neither sharply defined nor bordered by black, as in the models. The white apical spot is distinct, and the white spots in the hind margin of

* See R. Shelford in Poulton's "Essays on Evolution," 1908, pp. 351, 353.

the hind-wing come out in this Nymphaline as in the *Lycorea*. It also follows the *Lycorea* in the more ochreous shade of the yellow markings of the forewing.

With the object of showing more forcibly that these several species do actually occur together in one area, and have in many cases been caught on the same day, I have appended a list of the specimens collected in Brazil, between 1825 and 1830, by W. J. Burchell. It is a striking fact that one should have to go back to a collection eighty years old in order to gain the best available proof that these butterflies are associated together in space and time!

In addition to many members of both sub-divisions, Burchell took a fine series of the Pierine, *Perrhybris* (*Mylothris*) *pyrrha*, Fab. This species has not been included in the list on p. 591, because the apical spot is absent. Like all members of its genus, it is but a rough mimic, and, as regards the upper surface, a mimic only in the female. Just below the apical region, there is visible, near the hind margin of the fore-wing, the apparent incipient separation of a yellow spot from the oblique bar—a separation which is complete on the under surface. On this account the species is placed in the table of Burchell's captures as printed on p. 595, next to the sub-division with yellow apical spots.

H. W. Bates published the following interesting note on the habits of this species in his paper on the "Insect Fauna of the Amazon Valley" (*Journal of Entomology*, December 1861, pp. 235, 236): "It inhabits the shades of the forest; but the males are found also in open places, and resort to the moist margins of puddles and streams; the females I have never seen except within the forest; they are much rarer than the males, and are coloured in imitation of certain Heliconidæ* found in the same localities. The species has a wide range; it is common at Rio Janeiro and Bahia; specimens from those localities I find do not differ from those taken by myself in the Amazon region."

An interesting feature is noticeable in the hind-wing where the broad black margin is deeply serrated in its

* In the term "Heliconidæ," Bates included the *Ithomiinæ*, the *Lycoræini* (a section of the *Danainæ*) and the *Heliconinæ*. The two former he called "*Danaoid Heliconidæ*," and the third "*Acræoid Heliconidæ*."

LOCALITY.	DATE.	White apical spots in fore-wing.			Yellow apical spots in fore-wing.			No apical spots in fore-wing.		
		<i>Ceratinia euryanassa.</i>	<i>Ceratinia diæta.</i>	<i>Mechanitis lysimnia.</i>	<i>Protagonitis drwii.</i>	<i>Heliconius narcea.</i>	<i>Heliconius polyglottus.</i>	ITHOMINÆ.	DANAINÆ.	PIERINÆ.
Minas Gerães	Oct. 14, 1825	..	2	1 + [1] *
"	Oct. 15 "
"	Oct. 19 "	1	[1, Oct. 21]
"	Oct. 29 "	3	..	1 + [1, Oct. 30]
"	Nov. 4 "
"	Nov. 7 "	2
"	Nov. 10 "
"	Nov. 12 "	1	1
"	Nov. 12 "	1
"	Dec. 6 "
"	Dec. 31 "	1
"	Jan. 31, 1826
"	Feb. 8 "	1
"	Feb. 9 "	..	1	1 + [1]
"	Feb. 12 "
"	Feb. 16 "	1
"	Feb. 21 "	..	1
"	Feb. 28 "	1
"	Mar. 1 "	1
"	Mar. 7 "	1	..	2
"	Mar. 9 "	1	..	1 + [1]
"	Mar. 10 "	1
"	Mar. 13 "	1
"	Mar. 15-17 "
"	Mar. 19 "	1
"	Mar. 21 "	1 + [1]
"	April 1 "	[1]
"	Sept. 15 "	1
"	Sept. 26 "
"	Dec. 14 "	1
"	Dec. 16 "	1
"	Aug. 29, 1827
"	Oct. 2 "	1
"	Oct. 30 "
"	Dec. 24 "
"	Dec. 4, 1828	1
"	June 16, 1829
"	July 29 "
"	Dec. 10 "	1
"	No data.	1	1
Totals	12 + [2]	6	21 + [2]	1	10 + [5]	1	8 + [1]	3	27 + [2]

Numbers in square brackets denote the existence of specimens which cannot now be traced. Their data are contained in a list prepared under the direction of the late Professor Westwood.

* Two specimens with this date are recorded in Burchell's note-book as well as in Westwood's list.

costal region, resulting from invasions of the orange-brown ground colour. This suggests the possible transition from a special warning character or aposeme acquired by the *Perrhybris* on the way from the ancestral Pierine white towards this tawny and yellow, black-barred association. Slight traces of this same feature are visible in the *Dis-morphia* of this association; and the character is strongly marked in the female of *Perrhybris malenka* of the Guatemala-Nicaragua Combination (see Plate XXX, fig. 16).

The most perfect resemblance between any two species in the above table (in spite of the differently-coloured apical spots) is that between *Melinara ethra* and *Heliconius narcæa*: the likeness is exceptionally strong. Mention has been made already on p. 589 of the occurrence of a marginal row of white spots in both *Protogonius* and *Lycorea*, and of the further indication of resemblance seen in the buff-ochreous fore-wing markings which in these two species replace the usual striking yellow. In spite of the apical patch of *P. drurii* being white (while that of *L. halia* is ochreous) it seems probable that the *Lycorea* is the chief model of the Nymphaline.

The chief characteristic feature of this association—the yellow hind-wing band—appears independently in *Mechanitis lycidice* of Guatemala, which has already been shown to enter two of the Central American combinations (see p. 587). Many specimens of a fine series in the Hope Collection possess this yellow band in a well-developed condition. In other numerous specimens it is marked to a lesser degree, while in others again it is entirely absent, as we should expect in a member of the more northern combinations.

We now pass from a warning pattern characteristic of the country to the south of the Amazon mouths to a very different type developed beside its upper waters.

COMBINATION III. (Shown on Plate XXXII.)

The Upper Amazons (Ega) Type.

ITHOMIINÆ.

Tithorea harmonia, Cram.

Melinæa pardalis, Bates

(Fig. 3).

Melinæa pardalis, Bates, sub-

sp. nov. *madeira* (Fig. 2).

Mechanitis egaënsis, Bates

(Figs. 4 and 5.)

Ceratinia fluonia, Hew.

DANAINÆ.

Lycorea cinnamomea, Wey-

mer (Fig. 1).

NYMPHALINÆ.

Protogonius castaneus, Butl.

(Figs. 10 and 10a).

HELICONINÆ.

Heliconius pardalinus, Bates

(Figs. 8 and 9).

PIERINÆ.

Dismorphia egaëna, Bates

(Figs. 6 and 7).

The only addition to Blandford's list is a sub-species* of *Melinæa pardalis* from the Rio Madeira to the S.E. of Ega. The principal features of this association are the darkening of the ground colour into a mahogany or chestnut tint, and the mottled appearance of the outer half of the fore-wing, this latter effect produced by broken irregular yellow markings on a dark background. The black markings of the North-Central American type are still visible on the hind-wing, but they are more heavily developed and often tend to fuse together, as in the Guiana Combination. As usual, the *Melinæa* and *Heliconius* stand out as the central pair, *H. pardalinus* (Figs. 8 and 9) resembling *M. pardalis*, sub-sp. *madeira* (Fig. 2) in a most remarkable manner; but the whole of the Ithomiines form with the *Heliconius* and the *Dismorphia* (Figs. 6 and 7) a wonderfully close combination. The yellow spot at the anal angle of the fore-wing in the two species of *Melinæa* appears in the *Lycorea* (Fig. 1), while in the *Heliconius* two spots are placed at the apex of the hind-wing. In the natural position of

* A brief description of this form will be found in the Appendix on p. 604.

the wings during flight or at rest with wings expanded, the upper of these two is doubtless concealed and the lower spot then probably represents that on the fore-wing of the *Melinæa*. The male Pierine *Dismorphia egaëna* (Fig. 6) bears a similar spot at the apex of the hind-wing, and probably mimics the *Heliconius* in this respect. The *Protogonius* (Fig. 10), as before, is only a rough although a most unmistakable mimic, and as in the previous associations, the *Lycorea* (Fig. 1) appears to act as its principal model, both species being conspicuous in the combination for their hind-wing marginal spots and for the ochreous markings of the fore-wing.

The transition from this association to the next is probably in part preserved in a separate Peruvian association, in which the mahogany ground colour has been replaced by orange-fulvous; the black bands of the hind-wing have fused or half-fused, while the apical yellow markings in the fore-wing are much reduced and wanting altogether in some cases. Thus the three following Peruvian species would be considered obvious members of the Ega association except for the substitution of an orange-fulvous ground colour for the Ega mahogany tint. These are *Ceratinia anastasia*, Bates, a Peruvian form of *Melinæa pardalis*, Bates, and *Heliconius floridus*, Weym. All three species possess both yellow apical and black hind-wing markings, which are very similar to those of the species from Ega. A further stage in this transition is suggested by two species of *Melinæa* (*M. phasiana*, Butl., and *M. orestes*, Salvin), and one *Heliconius* (*H. arcuella*, Druce), in all of which the yellow apical markings are wanting. Except for this deficiency they resemble the former trio. *Tithorea cuparina*, Bates, may represent the next step; for in it the apical region is black and free from all traces of the mottled appearance. The black hind-wing, typical of the next association, is not however found in this *Tithorea*, which still retains the black bar placed upon an orange-tawny ground colour.

These interesting transitional forms lead on to the last Neotropical Association considered in this paper.

COMBINATION IV. (Shown on Plate XXXIII.)

The Bolivia, Ecuador and Peru type.

ITHOMIINÆ.

Melinæa mothone, Hew. (*cydippe*, Salv.)* (Figs. 1 and 2).

Mechanitis deceptus, Butler (*methone*, Salv., nec Hew.) (Figs 4 and 5).

Ceratinia semifulva, Salv.

Napeogenes achæa, Hew.

Hyposcada fallax, Staud. (Fig. 3).

SATYRINÆ.

Pedaliodes praxithea, Hew.
Pedaliodes triaria, G. and S.

NYPHALINÆ.

Protogonius semifulvus, Butl. (Figs. 14 and 15).

Eresia ithomiola, Salv. (Figs. 12 and 13).

Eresia murena, Staud.

HELICONINÆ.

Heliconius aristiona aristiona, Hew. (Figs. 6 and 7).

Eueides acacetes, Hew. (Figs. 8 and 9).

ACRÆINÆ.

Acraea acipha, Hew. (Figs. 10 and 11).

PAPILIONINÆ.

Papilio bachus, Feld. (Figs. 16 and 17).

HYPSIDÆ (Moth).

Pericopis hydra, Butl. (Figs. 18 and 19).

Castnia pellowia, Druce.

Blandford's list is here increased by *Hyposcada fallax*, the two Satyrines, *Eresia murena*, and the two moths, while *Napeogenes achæa* almost certainly represents his unnamed species of this genus.

In this large and interesting combination the original striped pattern has entirely disappeared, and the warning

* I here follow Butler's interpretation of Hewitson's figure of *Mechanitis mothone* in "Exotic Butterflies," vol. i, Pl. XLVII, fig. 14. Hewitson's type has not been discovered, but the figure appears to represent a male *Melinæa*, and not a female *Mechanitis*. Blandford's list adopts the synonyms.

appearance consists of a very dark ground colour crossed by a broad black-spotted band of orange-tawny, from the centre of the costa to the anal angle of the fore-wing and apex of the hind. Although a very strong general likeness runs through the whole combination, there are also close resemblances between special members, as for instance the large *Heliconius aristiona* (Figs. 6 and 7), which evidently follows *Melinæa mothone* (Figs. 1 and 2). The spots in the oblique band are superficially alike, while in both species there is very little orange-tawny colour at the apex of the hind-wing.

Another special internal association is formed by *Hyposcada fallax* (Fig 3) and *Eresia murena*, probably a southern form of *E. ithomiola*, Salv. Here the spots in the band are only two in number, both faithfully reproduced in *murena*. Again, as regards the orange-tawny area at the apical region of the hind-wing, the Ithomiine is followed by the *Eresia*. *Eresia murena* is not represented on Plate XXXIII; and the two forms of *Eresia ithomiola* ♀ there figured are not such close mimics of *H. fallax*. It will be seen by a glance at figures 12 and 13 on Plate XXXIII that the outer margin of the oblique tawny band becomes pale, due to the appearance of a yellow tint in these two *Eresias*, which on that account must be specially associated with the *Papilio* (Figs. 16 and 17), and moth (Figs. 18 and 19), considered on p. 601.

The *Protogoniüs* (Fig. 14) and the *Papilio* (Fig. 16) are rougher in their resemblance, and perhaps tend towards the *Heliconinæ* and especially the *Eucides* (Fig. 8), rather than the *Ithomiinæ* (Figs. 1-5).

An interesting feature of this *Protogoniüs* is the absence of white spots in the hind margin of the hind-wing. The reason is probably to be found in the absence of a *Lycorea* from this association. These spots may be considered as ancestral in the *Protogoniüs*—faint traces of them can still be detected even in *P. semifulvus*—and the presence of a similarly-spotted *Lycorea* in the associations tends towards their retention by the Nymphaline. In this combination (IV), however, in the absence of a *Lycorea*, the *Protogoniüs* loses its marginal spots and enters more closely than usual into the general mimetic association.

Professor Poulton has also pointed out to me that in Bolivian specimens of *Mechanitis deceptus*, small white sub-marginal spots are retained in the sub-apical region of the

under surface of the fore-wing, while these markings are absent or occasionally just visible in examples of the same species from Peru and Ecuador. Here the ancestral feature, obsolete in more northern localities, is preserved in the south. In some Bolivian specimens these spots extend round the hind margins of both wings.

Other species showing a closer resemblance within the association are seen in the moths, *Pericopsis hydra* (Figs. 18 and 19), *Castnia pellowia*, and the *Papilio* (Figs. 16 and 17). In all these, yellow markings appear at the costa of the fore-wing extending more or less completely along the outer margin of the oblique tawny band, and, except in the *Castnia*, yellow spots are developed along the hind margin of the hind-wing. These features are generally wanting from Combination IV, although, as regards the fore-wing, *Eresia ithomiola* ♀ (Figs 12 and 13) approaches the *Papilio* and the moths. The resemblance of the *Castnia* to *Papilio bachus* is much closer than that of the *Pericopsis*. The yellow outer border of the orange-tawny oblique band of the fore-wing in the above constituents of Combination IV, as also in the majority of the specimens of *Napcogenes achæa*, is undoubtedly transitional towards Blandford's "7. Central Colombian modification" of "6. Ecuador Type,"—the latter name being applied by him to the association now being considered. From the evolutionary point of view, however, the yellow fore-wing marking of the Central Colombian association is certainly ancestral, and its absence in Ecuador, etc., a comparatively recent modification. The relationship between these two combinations, distinguished by the presence or absence of the yellow margin to the oblique fore-wing band was clearly pointed out by H. W. Bates in the historic memoir on Mimicry (Trans. Linn. Soc., Lond., 1862, vol. xxiii, Pl. III, p. 514):—"Some of the close resemblances amongst the *Heliconidæ* themselves seem to be kept up by their varying in a precisely similar way. There is a very singular instance in three species of three different genera, *Melinæa*, *Mechanitis* and *Heliconius*, which are all in East Peru, orange and black in colour, and in New Granada orange, black and yellow. This seems to be a case of coincident, simple variation; for if three forms are quite alike in colours, it is conceivable that they may vary alike when placed under new conditions by migration. Our *Leptalides* have been shown not to vary precisely like their

models; and therefore the case just quoted does not throw any difficulty in the way of the explanation I have given; but it is a very extraordinary one."

This passage is a good example of the difficulties in which Bates was placed by the mimetic likeness between specially protected groups. Bates' suggested interpretation seems to indicate that the colour resemblances between the *Heliconinæ* and *Ithomiinæ* had obscured in his mind the essential structural differences between these widely separated sub-families. (See Poulton, "Essays on Evolution," 1908, p. 327.)

In each of the four combinations hitherto considered, the *Ithomiinæ*, *Heliconinæ*, and *Nymphalidæ* are all represented. Combination IV alone contains no Pierine or Danaine member. On the other hand, it provides us with an *Acræa*, two *Satyrinæ*, a *Papilio*, and a Castniid moth. No species belonging to any of these groups enter the three other associations.

The possibility of a single warning pattern gradually changing in the passage from one locality to another, *e.g.* from the brilliant striped pattern of the Guatemala-Nicaraguan type to the more sombre colour of the Ecuador, Peru, and Bolivia type, becomes conceivable when we find transitional stages. Thus we may imagine that the North-Central American type is an ancestral dominant warning pattern, and that on proceeding towards the south-east, the conditions gradually began to favour a darker hind-wing, as in the Guianas, and a yellow band and apical fore-wing markings, as in Eastern Brazil. The favourable conditions here referred to include above all the influence of changes in the patterns of the most dominant and central models in the combinations. Following these great associations westward, the apparent differences between the Ega Combination (III) and those of the East and North, is found to be consistent with an underlying similarity. Thus we here recognise in the black band of the hind-wing and the yellow apical markings of the fore, the characters of the North-Central American Combination (I). I have already mentioned instances showing possible transitional stages between the Ega type and the still more westerly association in Ecuador, Peru, and Bolivia.

The whole problem, however, can only at present be one of surmise, owing to the enormous amount of work still to be done in these areas, and more especially in the intervening districts; for until far more data have been accumulated than at present, we can only indirectly infer that certain members of the associations are dominant as compared with others; and it is impossible to feel much confidence in the selection of any single pattern as the ancestral type which has given rise to those of adjacent areas. These questions must remain open until further labours have thrown far more light upon this fascinating subject.

CERTAIN MÜLLERIAN COMBINATIONS AMONG THE DANAINÆ OF THE OLD WORLD.

The accompanying Plate XXXIV exhibits members of three small associations from Southern India, Fiji and the Solomon Islands respectively. The names and localities are indicated on the plate itself, and, in greater detail, in the explanation of plate. The colours and patterns are those characteristic of an important Eastern section of the *Danainæ*—the *Euplœini*. In the two first-named localities, certain species of this section are seen to resemble one another: in the third locality a species (Fig. 10) of the other important section of the *Danainæ*—the *Danaini*—has assumed the superficial appearance of an Euplœine (Fig. 5). It is unnecessary to speak in any detail of the associations represented on Plate XXXIV: they are only introduced on the present occasion for the striking comparison which they afford with the New World Combinations exhibited on the four preceding plates. I may, however, remark upon the interesting example of Fijian mimicry in Figs. 4 and 9. It is here obvious, as Professor Poulton pointed out to me, that the chief spot in the fore-wing of *Deragena proserpina* (Fig. 9) has been lengthened inwards so as to afford a superficial resemblance to the chief spot of its model *Nipara eleutho* (Fig. 4). Although the two chief elements of the pattern in these two Euplœines have thus attained a considerable degree of resemblance, it is certain that they belong to a different series of white markings,—sub-marginal in the mimic (Fig. 9), discal in the model (Fig. 4).

In these Old World Combinations no *Ithomiinæ* lead

the way, and their place is taken by the highly distasteful *Danainæ*, so dominant in the Oriental and Ethiopian Regions. In the former, both *Danaini* and *Euplecini* (here alone shown as models) are dominant; in the latter, the *Danaini*. The examples figured on Plate XXXIV are valuable for comparison with those from the New World; for they prove that, with an entirely different superficial appearance, the same bionomic principles are equally prevalent in the tropics of both hemispheres. The *Danainæ* of the Old World represent and take the place of the *Ithomiinæ* in the New, and exhibit, although with very different colours and patterns, the same conspicuousness at rest and in flight, the same countless swarms of individuals, the same Müllerian resemblances between dominant species, and the same mimetic attraction for less abundant species of other groups.

APPENDIX.

Melinæa pardalis, Bates, n. sub-sp. *madeira*.

Melinæa madeira appears to be a MS. name of Staudinger's. Professor Poulton and Mr. F. A. Heron have very kindly spent much valuable time in an endeavour to trace a description of it, but without success. Thinking that the discrimination of this sub-species of *Melinæa pardalis*, Bates, may be a convenience to naturalists, a description is here added.

Melinæa madeira, n. sub-sp.

This sub-species differs from *M. pardalis*, Bates, in the following points on the upper side. *Fore-wing*: the thick black inner marginal border of *pardalis* (which is limited by the median nervure and first median nervule) is reduced to a narrow, superiorly somewhat diffuse, dark marginal edging in *madeira*. The large triangular black spots, one below the outer part of the cell and the other in the basal part of the cell itself, are reduced by more than half in *madeira*. Exterior to these spots in *madeira* are two yellow oblique angulated bands joined about the second median nervule; in *pardalis*, however, the inner one has become suffused with the mahogany ground colour (with the exception, in one example, of a

single yellow spot just under the sub-costal nervure). In the type of *madeira* (Fig. 2) the apical markings of the fore-wing of *pardalis* are nearly obliterated by a fuscous suffusion, but in another example at Oxford they persist almost as in the Ega form. The yellow spot at the anal angle in *madeira* is well developed, being larger than in *pardalis*. *Hind-wing*: the black bar across the hind-wing so strongly developed in *pardalis* is much reduced in *madeira*, and does not reach the inner margin. All its constituent markings in *madeira* are somewhat rounded and give a less continuous appearance than the compact bar and marginal border of *pardalis*. This latter is also greatly reduced, being much narrower and more completely divided into its constituent markings. On the under side the same points of difference occur as on the upper; although the black markings in the fore-wing of *pardalis* are here not quite so obviously heavier than those of *madeira*. A noticeable difference in the fore-wing is the appearance, along the hind-margin (above the anal spot), in *madeira* of four (in one specimen) small pale-yellow spots which are absent in *pardalis*. In the second specimen the spot nearest the apex is barely distinguishable.

Type ♀ in Hope Department, University Museum, Oxford (Plate XXXII, fig. 2).

Distribution, based on two ♀ specimens in Hope Department, with the general locality Amazons, and one ♂ and two ♀ in the British Museum from Manicoré, on the Rio Madeira, the most important southern tributary of the Amazon.

In another specimen of *M. pardalis*—probably taken higher up the Amazons in Northern Peru or Ecuador—a more chestnut-fulvous ground colour takes the place of the mahogany tint, and the sub-apical markings lose much of their yellow shade. The yellow spot at the anal angle of the fore-wing is still more obscured. The presence of this chestnut-fulvous colouring shows a transition into other Peruvian forms in which this change is carried still further.

H. W. Bates (Trans. Linn. Soc., Lond., 1862, vol. xxiii, part iii, p. 552) makes an interesting note on this very point. He writes: "I did not meet with *M. pardalis* at S. Paulo; but at Tabatinga, eighty miles further west, it again occurred, not however under precisely the same form as at Ega, but in a modified state, the yellow

cross-belt and the spot at the hind angle of the forewing having become of the same dark orange-brown hue as the rest of the wing. The same transformation of colour takes place in many species of *Heliconidæ* in travelling from east to west, and I am inclined to think it is due to the direct action of the physical conditions of the localities on the early states of the insects."

M. madeira must be considered a south-eastern form of *M. pardalis*, whose chief habitat is at Ega, on the Upper Amazons.

It should be observed that in this description two ♀♀ of *M. madeira* were compared with two ♂♂ of *M. pardalis*.

My sincere thanks are due to Mr. R. Trimen, F.R.S., for his kind help in the above description.

EXPLANATION OF PLATES XXX—XXXIV.

[See *Explanation facing the PLATES.*]